# **Occasional Papers On Mollusks**

Published by

THE DEPARTMENT OF MOLLUSKS Museum of Comparative Zoology, Harvard University Cambridge, Massachusetts

VOLUME 3

FEBRUARY 6, 1970

NUMBER 39

# The Genus *Priotrochatella* (Mollusca: Helicinidae) of the Isle of Pines and Jamaica, West Indies

By WILLIAM J. CLENCH AND MORRIS K. JACOBSON

*Priotrochatella*, a genus in the Helicinidae, was established by H. Fischer in 1893 for the type-species, *Helicina constellata* Morelet 1847, which is characterized by its striking pagodalike shape and the extravagant surface ornamentation. The genus is endemic to the Isle of Pines and Jamaica. On the Isle of Pines the shells occur in large numbers in their restricted habitat in a small area of the north central part near the city of Nueva Gerona (pl. 21). We have been able to examine large series of shells in various museums.

Morelet localized constellata in the "Sierra de Cristalles" [sic]. Clapp (1918: 48) showed that this must have been an error since the only Sierra de Cristales on the island is in the south where the rock is igneous and few land mollusks occur. Clapp further pointed out that Poey transposed the names Sierra de Casas and Sierra de Caballos, and it was Arango (1878: 45) who first properly restricted the locality of constellata in the Sierra de Casas, west of the town of Nueva Gerona. The three species on this island are apparently well localized, as explained by Clapp (p. 49) and borne out by the lots of shells we were able to examine, as follows: constellata in the northern portion of Sierra de Casas; torrei Clapp on the southern section: and stellata Poev in the Sierra de Caballos on the eastern side of the Río Casas. Clapp (l.c.) believed that stellata might also be found in the northern extension of the Sierra de Caballos "now called the Sierra de Columbus". Directly to the south of Sierra de Caballos and apparently completely separated from it, since a straight road is shown running between the two sections, lies the Sierra Chiquita of which we have found no mention in the literature or on collection labels.

The striking peripheral serration of the shells of *Priotrochatella* is nearly unique. A few species from southeast Asia, *Calybium mouhoti* Pfeiffer and *C. martensi* Issel have shells which are startlingly similar, but the apparent serrations of the latter result from regular undulations of the thin peripheral keel, while those in *Priotrochatella* are independent calcareous extensions.

Observers have previously noted similarities between shells from the Antilles and from southeast Asia in other groups as well, e.g. *Pupinella* and *Farcimen*, and in several camaenids. In the case of several species of *Eutrochatella s.l.* from the Cuban mainland the shells are incrusted with a layer of inorganic matter which occasionally assumes the shape of the marginal denticulations of *Priotrochatella*.

In 1922, H. B. Baker published a valuable study of the radulae of helicinids which established a sound foundation for the family. He demonstrated certain fundamental differences upon which the superspecific categories definitely can be based. Baker characterized the Eutrochatella radula as follows (1922: 58): central tooth complex, consisting of seven plates, as well as a large T-lateral, generally without cusps, 56 to 111 uncinals; and 123 to 191 teeth per row. The Troschelviana-like radula is characterized as: central tooth complex and T-lateral cusped: 44 to 64 uncinals; and 99 to 111 teeth per row. The "smooth" Eutrochatella-like radula is found in Calybium Morelet from southeast Asia as well as in Eutrochatella Fischer in the West Indies. Hence the assumption is not unwarranted that the "smooth" radula is more ancient than the cusped one and that the cusped radula of the Cuban Troschelviana represents a later development. If this is so, we may regard Priotrochatella as a relic form or more likely an immigrant of an early group which, in addition to the smooth radula, also shows a highly sculptured shell suaface.

All the specimens examined in the course of this study are in the collection of the Museum of Comparative Zoology, Cambridge, Massachusetts. Date references to Wagner in the

### OCCASIONAL PAPERS ON MOLLUSKS

Conchylien-Cabinet follow Smith & England (1937: 91-92).

#### ACKNOWLEDGMENTS

We wish to express our gratitude to Drs. Joseph P. E. Morrison and Joseph Rosewater of the United States National Museum for providing us with pertinent loan material. Drs. Kenneth J. Boss and Ruth D. Turner of the Museum of Comparative Zoology read the manuscript critically and made valuable suggestions. Mr. J. F. Peake of the British Museum (Natural History) was good enough to supply us with the figures and the catalog number of the type of *Helicina constellata* Morelet. This work was done with the support of NSF Grant GB-1004.

# Genus Priotrochatella H. Fischer

Priotrochatella H. Fischer 1893, Jour. de Conchyliologie, **41**: 88 [as a subgenus of *Eutrochatella*]. [Type-species, *Eutrochatella constellata* (Morelet) 1847, monotypic].

Description. Shell depressed turbinate, carinate, surface sculpture of variously strong axial and somewhat weaker spiral cords, basal sculpture strong to obsolete. Whorls ornamented peripherally with a more or less strongly denticulated flange, widest on the body whorl. Protoconch smooth, papilliform, sharply raised. Operculum thin, dished, kidney shaped; outer calcareous layer white, variously strong, surface either papillose or smooth, the palatal margin lamella-like, strongly raised and separated from the inner layer; inner layer very thin; transparent, brownish, extending well beyond the edge of the outer layer except at the columellar margin.

*Remarks.* This genus is confined in the Isle of Pines to the sierras in the north central part on both sides of the town of Nueva Gerona. Wagner's statement (1907: 16), repeated by Thiele (1929: 83), "Auf der Insel Cuba" is not correct. We are also including *P. josephinae* C.B. Adams from Jamaica in this genus. The reasons for this we state below.

H. Fischer (1893) considered *Priotrochatella* a subgenus of *Eutrochatella*, where it was kept by Wenz (1938: 436), Thiele (1929: 82) and Keen (1960: 288). Wagner (1907: 16) and Clapp (1918: 50) raised the group to generic rank. Clapp wrote, "The radula of the three species... exhibit sufficient differences in

63

structure from other groups of Helicinidae to sustain the raising of *Priotrochatella* to generic rank." H.B. Baker (1922: 61), who had studied the radulae of *stellata* and *torrei*, found them to be identical with the radula of *Eutrochatella*, restricted, except that the "R-central tooth is broadly elliptical instead of circular." He continued, "The separation of this group from *Eutrochatella sensu stricto* even as a subgenus, is only justifable on the grounds of the peculiar shell and opercular characteristics." We have chosen to preserve the name *Priotrochatella* as a genus viewing it as basically a Jamaican group which was introduced into the Isle of Pines early enough to have broken up into three related species.

### Priotrochatella constellata (Morelet) Plate 17, figs. 1–4

*Helicina constellata* Morelet 1847, [*in*] Guerin-Meneville, Revue Zoologique, Paris, **10**: 144 (sur les rochers de la Sierra Cristalles, l'Isla de Pinos, au sudouest de Cuba). [Types in British Museum, no. 1893.2.4.1609-1611.]

Helicina constellata Morelet 1849, Testacea Novissima Insulae Cubanae et Americae Centralis, Paris, 1: 21 (rupestris insulae Pinorum).

*Helicina pagoda* "Velasquez" Pfeiffer 1852, Monographia Pneumonopomorum Viventium, p. 334 (nomen nudum).\*

Trochatella constellata Morelet. Sowerby 1866, Thesaurus Conchyliorum, 3: 296, pl. 278, fig. 450.

Priotrochatella constellata Morelet. Wagner 1907, [in] Martini & Chemnitz, Conchylien-Cabinet (2) 1: sect. 18, pt. 2, p. 16 [not figured].

*Description.* Shell reaching about 12.5 mm. in diameter, 8.5 mm. in height, depressed turbinate, rough, moderately strong. Basic color lemon-yellow, occasionally brownish, with irregular white patches; sculpture white, base yellow, white in umbilical region, protoconch and serrated peripheral flange white. Whorls 8, flat, carinate, slowly increasing in width, the later whorls armed peripherally with a strongly denticulated, shelv-

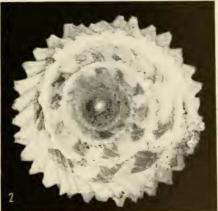
<sup>\*</sup> The MCZ collection has one lot (50953) bearing the label *Trochatella pagoda* Vel. from the Anthony Collection. This "type" of a *nomen nudum* proves to be identical with *P. constellata*.

Figs. 1-2. *Priotrochatella constellata* (Morelet), MCZ 127430, Sierra de Casas, ex Bermúdez Collection (both  $3.5 \times$ ).

Figs. 3-4. *Helicina constellata* Morelet, 2 of the 3 syntypes, British Museum 1893.2.4.1609-1611, Isle of Pines (both  $2.5\times$ ).

# OCCASIONAL PAPERS ON MOLLUSKS 65







ing flange, widest on the body whorl; the serrated keel of the body whorl is sharply set off from that of the penultimate whorl, giving a pagoda-like appearance to the shell. Suture shallow, covered on the later whorls by the peripheral serrations of the preceding whorl. Spire above the penultimate whorl low, apex sharply raised. Aperture strongly oblique, longer than wide, evenly rounded below, distorted palatally by the serrated carina of the body whorl. Parietal wall slightly swollen, strongly sculptured; with a thin, white, sublustrous parietal wash, unevenly rounded at outer margin. Outer lip flat or rounded, widened, slightly flaring, more so below the carina. Columella short, curved, white, widest above, arching shortly over the closed umbilical pit. Sculpture of the postnuclear whorls of thin, widely spaced, retractive axial cords, growing stronger on the later whorls, where they constitute the upper margins of the peripheral serrations. Spiral sculpture of slightly raised, thin cords generally arranged in series of 2 or 3 in the center of the whorls; base weakly inflated, strongly cancellated by equally strong spiral and axial cords, the axial cords extending basally to the tip of the serrations. This sculpture weakens as it approaches the umbilical area but persists in the aperture. Protoconch smooth, white, papilliform, sharply raised. Periostracum wanting. Operculum as in subgenus, outer layer thick, papillose.

height	diameter	
8.2 mm.	12.5 mm.	Sierra de Casas
8.1	12.2	Sierra de Casas
8.7	12.2	Sierra de Casas

*Remarks.* All the lots of this species which we have examined bear only the locality of Sierra de Casas (but see remarks under *Priotrochatella*, p. 63). It has been frequently found here by many collectors (Morelet, Gundlach, Brooks, Barbour, etc.) each of whom usually took large series. We have looked in vain for published ecological notes. From the shape and structure of the shell, it may be assumed that this is a species found almost wholly on rocks like most *Eutrochatella*.

The shells vary little and are easily recognized by the double periphery in mature shells, the upper one of which is frequently wider than the lower one on the body whorl. Hence the major diameter is taken not by measuring the body whorl, which is inset, but rather the penultimate.

### Priotrochatella torrei *Clapp* Plate 18, figs. 1–2

Priotrochatella torrei Clapp 1918, Nautilus, **32:** 47, pl. 4, figs. 1, 2, 5, 6 (southern end of eastern face of Sierra de Casas, Isle of Pines). [Holotype, MCZ 36888, Sierra de Casas, Isle of Pines, Cuba; Paratypes, MCZ 50955 from the same locality].

Description. Shell reaching 7.7 mm. in height, 12.5 mm. in diameter, depressed, turbinate, somewhat convex, imperforate, carinate and dull. Base color lemon-yellow with irregular white patches, base yellow, white near aperture, peripheral flange and protoconch white. Whorls 9, slightly convex, slowly increasing in width, body whorl barely descending at aperture. Later whorls armed peripherally with a rather weakly denticulated, shelving flange, the denticulations weaker and more numerous than in either constellata or stellata. Suture shallow, in the later whorls covered by the serrations of the preceding whorl. Spire low, rounded, apex sharply raised. Aperture oblique, twice as long as high, distorted at the outer margin by the carina of the body whorl. Parietal wall weakly inflated, almost smooth, with a raised glassy callus, unevenly rounded at the outer margin. Palatal lip either flat, widened, or in some specimens double, the inner rounded lip widening at the periphery, obsolete above. Columella short, curved, widened above, arching shortly over the closed umbilical pit, slightly twisted at the insertion of the basal lip. Base smooth, barely marked by weak, curved, diagonal growth lines, no spiral sculpture. Spire with spiral sculpture of 4 or 5 relatively strong ridges, the lower two on the penultimate and body whorls obliquely cancellated by the axial cords, the axial cords running into the upper margins of the serrations. Protoconch smooth, white, sharply raised, papilliform. Periostracum wanting. Operculum as in genus, outer layer thin, glassy, smooth, margins moderately raised.

height	diameter	
7.7 mm.	12.4 mm.	Sierra de Casas, Holotype
7.4	12.2	Sierra de Casas, Paratype
7.6	12.5	Sierra de Casas, Paratype

*Remarks.* This species is easily separated from *constellata* by its inflated turbinate rather than pagoda-like appearance, by its more numerous and weaker peripheral serrations and

- Fig. 1. *Priotrochatella torrei* Clapp, Paratype, MCZ 50955, Sierra de Casas, Isle of Pines, Barbour & Brooks leg.
- Fig. 2. Priotrochatella torrei Clapp, Holotype, MCZ 36888, Sierra de Casas, Isle of Pines, Barbour & Brooks leg. (both 3.5×).

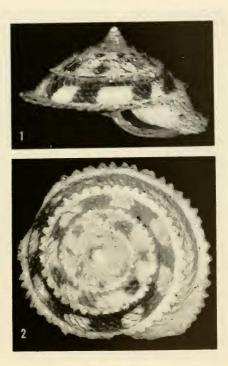


Plate 18

its smooth base. From *stellata* it differs largely in the smooth rather than axially ribbed base, and in the relatively weaker serrations. As Clapp has shown, it inhabits the southern end of the Sierra de Casas on the western side of Río Sierra de Casas, a mountain range which it shares with *constellata*. The latter, however, occurs only on the northern end. For its relationship with its congeners see remarks under *stellata*.

### Priotrochatella stellata (Poey) Plate 19, figs. 1–2

Helicina stellata Velásquez 1850, [in] Jay, Catalog of the Shells Contained in the Collection of John C. Jay, 4th ed., p. 262 (nomen nudum).

Helicina rota Newcomb, Jay 1850, ibid., p. 262 (nomen nudum).

*Helicina stellata* "Velásquez" Poey 1851, Memorias Historia Natural de la Isla de Cuba, **1:** 117, pl. 5, figs. 18-20 (en la Isla de Pinos, sobre la Sierra de Casas [sic], falda del Sud, Velásquez leg.]. [Type in Museo Poey, not seen.]

Trochatella stellata Velásquez. Sowerby 1866, Thesaurus Conchyliorum, 3: 296, pl. 278, fig. 451.

Priotrochatella stellata Velásquez. Wagner 1907, [in] Martini & Chemnitz, Conchylien-Cabinet, (2) 1: sect. 18, pt. 2, p. 17, pl. 1, fig. 3, pl. 2, figs. 12, 13.

*Eutrochatella (Priotrochatella) stellata* Poey. H.B. Baker 1922, Proc. Acad. Nat. Sci. Philadelphia, **74**: 61, pl. 6, fig. 30 [radula].

Description. Shell reaching 7.8 mm. in diameter, moderately strong, depressed trochiform, somewhat convex, lusterless, and carinate. Base color lemon-vellow with irregular white patches, base yellow, white toward the aperture; protoconch and serrated carina white. Whorls 9, increasing slowly in width, slightly convex, body whorl barely descending at aperture. Later whorls armed peripherally with a rather strongly but narrowly serrated flange widest on the body whorl. Suture shallow, covered in later whorls by the peripheral denticulated flange of the preceding whorl. Spire low, somewhat convex, apex raised. Aperture oblique, length about twice the width, well distorted at the palatal margin by the carina of the body whorl. Parietal wall slightly inflated, lightly sculptured, with a thin, glassy, parietal wash, unevenly rounded at outer margin. Palatal lip thickened, either rounded or flat, widest at the keel, narrower above Columella white, short, curved, widest above, arching shortly over the closed umbilical pit, twisting slightly at insertion of the basal lip. Spire and base with strong, arched irregularly spaced axial ridges, crossed by

weaker, more or less regularly spaced, spiral ridges, the axial ridges forming the upper margin of the denticulations; spiral sculpture wanting on the denticulated flange. Protoconch white, smooth, sharply raised, papilliform. Periostracum lacking. Operculum not seen, presumably as in the genus.

height	diameter	
7.6 mm.	12.7 mm.	Sierra de Caballos
7.4	13.0	Sierra de Caballos
7.8	12.5	Sierra de Caballos

*Remarks.* This species is most easily separated from the other two species of *Priotrochatella* by the nature of the basal sculpture. This is not as strongly cancellated as in *constellata*, since the spiral cords are weaker than the axial ridges, nor is it smooth as in *torrei*. In the strength of the denticulations of the flange, it similarly stands between *constellata* and *torrei*, these being weaker and somewhat more numerous than is the case in the former, but stronger and less numerous than in the latter. It occurs in the Sierra de Caballos on the eastern side of Río Casas from Sierra de Casas, the locality of its two congeners. Clapp (1918: 49) remarked on the peculiarity that though stellata in shape seems to be closer to torrei, it inhabits an area isolated from Sierra de Casas, the locality of constel*lata* and *torrei*. However, he reported that the central radular teeth of the latter two are closer to each other in their smaller size rather than to *stellata* which has a wider central tooth. Clapp also felt that the radula of *Priotrochatella* is sufficiently different to justify generic rank, an opinion opposed by H. B. Baker (1922).

All the lots we have examined bear only the locality Sierra de Caballos.

# Priotrochatella josephinae (C. B. Adams) Plate 20, figs. 1–2

*Helicina (Trochatella) josephinae* C. B. Adams 1849, Contributions to Conchology, **1:** 14 ([eastern part of] Jamaica), [Lectotype, here selected, MCZ 222614, ex C.B. Adams, J.G. Anthony Collection; Paralectotypes, MCZ 222615, from the same collections].

Trochatella josephinae pulchra C.B. Adams 1851, ibid., pp. 136, 181 ([western part of] Jamaica) [Lectotype, here selected, MCZ 222616, C.B. Adams Collection ex E. Chitty].

Trochatella josephinae Adams. Pfeiffer 1852, Monographia Pneumonopomo-

Plate 19

Figs. 1–2. Priotrochatella stellata Poey, MCZ 50954, Sierra de Caballos, Isle of Pines, ex Anthony Collection (both 3.5×).

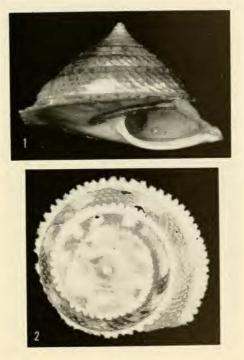


Plate 19

# 74 OCCASIONAL PAPERS ON MOLLUSKS

- Fig. 1. Priotrochatella josephinae pulchra (C.B. Adams), Paralectotype, MCZ 222615, Jamaica, E. Chitty leg., ex C.B. Adams Collection.
- Fig. 2. Priotrochatella josephinae (C. B. Adams), Lectotype, MCZ 222614, Jamaica, C.B. Adams leg., ex Anthony Collection (both 3.5×).

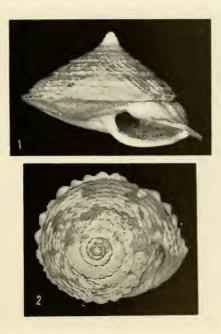


Plate 20

rum Viventium, 1: 335; Sowerby 1866, Thesaurus Conchyliorum, 3: 296, pl. 278, fig. 449.

*Eutrochatella (Eutrochatella) josefinae* [sic] C.B. Adams. Wagner 1908, [*in*] Martini & Chemnitz, Conchylien-Cabinet, (2) **1:** sect. 18, pt. 2, p. 107, pl. 20, figs. 12–14.

Description. Shell reaching about 12 mm. in diameter, strongly depressed trochoid, moderately thin, lusterless, carinate and base almost flat. Color pale, translucent, greenish yellow, interspersed with large irregular, opaque white areas, yellowish color generally lighter on body whorl and base; aperture and lip white. Whorls about 6, flat except for the weakly convex body whorl, carinate and widely, subregularly serrate, the serrations stronger on the later whorls. Suture well impressed, covered by the serrated carina of the preceding whorl. Spire low conic, body whorl somewhat swollen, apex raised. Aperture almost parallel with the base, rounded triangular, parietal angle widely rounded, palatal angle formed by the termination of the peripheral carina. Parietal wall almost flat, not excavated, with a lustrous, transparent, weakly raised parietal callus which is highest near the umbilical region and evenly rounded at the outer margin. Palatal lip well reflected basally below the carina, forming a pseudo-chink at the insertion of the body whorl: simple, sharp above, very weakly flaring near the periphery. Columella concave, evenly rounded, inserting gradually in the basal lip. Sculpture of deep, strongly curved, diagonal axial striae, crossed by generally well raised spiral cords, which are irregularly cut by the axial striae and irregularly ornamented with strong, raised, rounded, elongate, white tubercles, these tubercles merging into the serrations of the whorls. Base relatively smooth, marked by weak, axial growth lines and faint, closely spaced spiral cords. Protoconch  $1\frac{1}{2}$ whorls, white, rounded, microscopically pitted. Periostracum wanting. Operculum subrhomboid, twisted laterally; outer layer white, translucent, with a white, raised, minutely punctate lamella at the parietal margin, highest above. Inner layer thin, very pale brown, nucleus central, somewhat removed from the columellar edge.

76

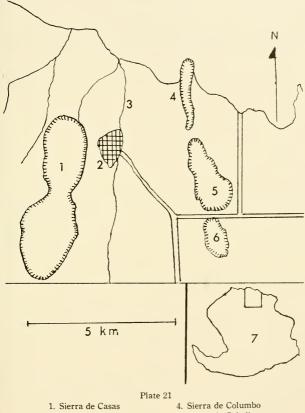
height	diameter	
7.2 mm.	12.6 mm.	Jamaica
6.7	11.1	Jamaica
8.3	11.8	Paratype
6.2	9.4	44
6.4	9.8	Lectotype
7.9	13.1	Lectotype of var. pulchra
6.2 6.4	9.4 9.8	Lectotype

*Remarks.* This species is quite uniform in appearance, the greatest variation being in size. The colors reported by Adams were not seen in the shells available for this study. The spiral sculpture likewise varies from ridges which are quite uninterrupted and conspicuous to ones less conspicuous and strongly interrupted by deep axial ridges and irregular nodules. Adams called the second group *pulchra* and stated that it came from the western part of the island. He reserved the name *josephinae* for the specimens with more regular spiral sculptures which he wrote came from the eastern part of Jamaica. We find lots, however (MCZ 22611 Chitty leg.), without locality which include specimens varying in this respect, many presenting various degrees of intergrade.

Much of the material collected by either Adams or Chitty has not been more precisely localized than merely Jamaica. Nor have subsequent students apparently been able to report it from more precise locations. Baker (1935) did not find it and Pilsbry and Brown (1910) do not report it from Mandeville. Hence it is impossible to localize the species at the present time or to evaluate the significance of the polymorphic populations.

The shells resemble those of *Priotrochatella*, especially *P. stellata* very closely, the chief difference being in the shape of the operculum. Baker (1922: 61) wrote of the operculum of *Priotrochatella*, "I regard it as simply a specialized condition of the *Eutrochatella*-operculum, due to the shape of the aperture." The radulae of *Priotrochatella* and *Eutrochatella* are practically the same, according to the same author. Hence we feel that *josephinae* should be included in the genus *Priotrochatella*.

This close relationship between a species from Jamaica and several forms on the Isle of Pines can well be the result of some form of mollusk transportation. Darlington (1957: 17–20) graphically described the unbelievable capacity of the wind to transport large amounts of material great distances. This may have been one of the agencies that brought the Jamaican form to the Isle of Pines. Clench (1938: 486 f.) suggested this as well as other means of transport. The possibility of rafting cannot be completely overlooked, since the currents in that portion of the Caribbean flow in a northwesterly direction, i.e. from Jamaica toward the western portion of Cuba. The introduction, if it did occur, must have been relatively early, since the Jamaican immigrant developed into three well distinguished Cuban descendants.



- 2. Nueva Gerona

- 5. Sierra de Caballos
- 3. Río Sierra de Casas 6. Sierra Chiquita 7. Isle of Pines showing area enlarged.

(After Military Map of the Republic of Cuba, 1932, sheet 5).

### BIBLIOGRAPHY

- Baker, H. Burrington, 1922. Notes on the Radula of the Helicinidae. Proc. Acad. Nat. Sci., Philadelphia, 74: 29–67, pls. 3–7.
- —, 1935. Jamaican Land Shells. Nautilus, 48: 6–14, 60–67, pl. 2.
- Clapp, William F., 1918. A New Priotrochatella from the Isle of Pines. Cuba, Nautilus, 32: 47–51, pl. 4.
- Clench, William J., 1938. Origin of the Land and Freshwater Fauna of the Bahamas, etc. Bull. Mus. Comp. Zool., **80**: 481–541.
- Dance, S. Peter, 1966. Shell Collecting. Univ. of California, Berkeley, 344 pp., 35 pls., 31 text figs.
- Darlington, Philip J., Jr., 1957. Zoogeography: the Geographical Distribution of Animals, New York, 14+675 pp., 80 figs.
- Fischer, H., 1893. Notes sur quelques points de l'histoire naturelle du genre *Eutrochatella*. Jour. de Conchyliologie, **41**: 85–89, pl. 3.
- Fulton, Hugh C., 1920. Molluscan Notes IV. Proc. Malac. Soc. London, 14: 3-4.
- Keen, Myra, 1960. [in] Treatise on Invertebrate Paleontology. Univ. of Kansas, pp. 285–288, figs. 186–187 (Helicinacea).
- Smith, Edgar H. & H.W. England, 1937. Jour. Soc. Bibliography Nat. Hist., 1: 89–99.
- Thiele, Johannes, 1929. Handbuch der systematischen Weichtierkunde, 1: 80-91, figs. 57-67 (Helicinidae).
- Wagner, Anton, 1907–1911. [*in*] Martini & Chemnitz, Conchylien-Cabinet, (2) 1: sect. 18, pt. 2, 391 pp., 70 pls.
- Wenz, W., 1938. [*in*] Handbuch der Paläozoologie, **6:** pt. 1, pp. 435–448, figs. 1071–1118 (Helicinidae).